



Force of Ciliary Motion

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one in the east wall opening into the hall. The furniture of the room consisted of a bed, wash-stand, table, and the trunk which contained the instrument of death, and which, on account of its construction and *modus operandi*, has been called "the Moon guillotine." The essential parts of the instrument are a broad-axe and lever screwed at one end to the floor. The axe was secured to this lever, seven feet in length, the lower two-thirds of which consisted of wood, by upright pieces of bar-iron fastened with bolts and screws. The lever was composed of three separate parts, for convenience in transportation, firmly bolted together, the widened end being attached to the floor by means of hinges to prevent any possible lateral motion. At the other end of the lever, the iron bars to which the axe was attached were very heavy, in order to give the machine great effectiveness when put in motion. The axe being elevated, was sustained at the proper angle for falling the greatest distance possible by means of a double cord attached to the free end of the lever, and to a small hook in a bracket, which was securely fastened to the wood on the side of the window, about five feet from the floor. On this bracket was placed a lighted candle between the cords, which were consumed when the candle had burned sufficiently. The axe being then unsupported, fell to do its fearful execution.—*American Practitioner*, August.

FORCE OF CILIARY MOTION. By H. P. BOWDITCH, M.D., Professor of Physiology, Harvard Medical School.—Most observers who have studied the movements of cilia have directed their attention to the evidence of ciliary activity afforded by the rapidity with which very light bodies are carried over the surface of the ciliated membrane. Thus Valentin (Wagner's Lexicon, i. 506) observed that the globules of mucus on the gills of anodonta were carried forward at the rate of four m.m. in one minute. Engelmann (Flimmerbewegungen, p. 70), in studying the various conditions which affect ciliary activity, made observations on the rapidity with which a small globule of sealing-wax, suspended by a light silk thread so as to merely touch the membrane, was moved forward over the ciliated surface. The rate varied in his observations from 7·8 to 24·5 m.m. in one minute. Calimburces (*American Naturalist*, v. 611) also, in constructing his apparatus for measuring ciliary movement, made all the parts as light as possible, in order to reduce the work done by the cilia to a minimum.

The late Jeffries Wyman (Bernard, *Les Tissues Vivants*, p. 141) was the first to call attention to the fact that the force exerted by cilia is by no means inconsiderable. He describes his experiments on frogs as follows: "The mucous membrane, being carefully dissected from the roof of the mouth, is pinned to a board. A piece of skin from near the throat of the frog, and from one third to half an inch square, is placed upon this membrane with the inner surface in contact with the cilia, it being kept in mind that these

vibrate from before backwards towards the throat. On the skin may be placed a plate of lead of somewhat smaller size. This serves as a vehicle to which weights may be added at will to increase the load. . . . Pains should be taken to have the board on which the experiment is made perfectly horizontal, otherwise a sliding motion, especially when heavy weights are used, may come in to vitiate the experiment." The rate of movement was determined either by direct observation of the lead "vehicle" with its load, or by means of an index attached to the axle of the smaller of a pair of light cog-wheels, the "vehicle" being connected with the apparatus by means of a thread coiled round a drum on the axle of the larger wheel. By experiments performed in this way it was found that a weight of 1.3 grammes was carried fifteen m.m. in about one minute, the weight resting on a surface of twelve m.m. square, and that "forty-eight grammes, resting on a surface fourteen m.m. square, moved, though very slowly, across the whole length of the membrane; but the exact time was not noted."

It will be noticed that in these experiments the work done by the cilia consisted in overcoming the friction of the skin upon the membrane and of the parts of the index-apparatus on each other, and that the amount of this work, though increased by the addition of weights to the lead plate, was not, and could not well be, accurately determined. The weight being moved in a horizontal plane, there was no direct performance of work which could be measured by foot-pounds or kilogrammetres. In view, however, of the evidently very considerable force of the ciliary movement, it seemed important to determine the maximum of work which could be performed in a given time by a given surface of ciliated membrane. The simplest way of accomplishing this object seemed to be to repeat Wyman's experiments, with the modification of giving to the board on which the membrane rested an inclination which would compel the cilia to move a weight resting upon them up an inclined plane. Then the product of the weight by the height through which it was lifted would give the value sought.

After several preliminary experiments an apparatus was constructed, consisting of a piece of thin board about eleven c.m. square, with a narrow strip of wood, about seven m.m. in thickness, fastened at the middle of one edge. A strip of glass 4.5 c.m. long, by one c.m. broad, with edges smoothed on a grindstone, was firmly cemented by one end to the middle of the strip of wood, and thus projected over the surface of the board, parallel to, and 7 m.m. from it. A frog with brain and spinal cord destroyed was then prepared as follows: a transverse incision, about one c.m. long, was made through the mucous membrane of the roof of the mouth as far forward as possible. The free end of the glass strip was inserted into this incision, and pushed back between the membrane and the bones of the palate. The lower jaw was then cut away, and the oesophagus laid open as far as the stomach. The cut edges

of the œsophagus were kept extended by pins thrust through them into the board below. The frog thus lay upon the board with the body under the strip of glass, and the ciliated membrane from the anterior edge of the palate to the stomach smoothly stretched over it and accessible to observation and experiment. A vehicle to be moved by the cilia was made by cementing a small oval piece of glass of 1.437 square c.m. area to a thin piece of wood of the same size. The glass surface was then covered with a piece of frog's skin stretched over it, with the inner surface outward, and held in place by a thread tied round it and lying in a groove cut in the edge of the wood. This vehicle, when placed with the skin downward upon the ciliated membrane, was readily carried along towards the stomach. The work done by the cilia could be increased either by placing weights upon the vehicle or by inclining the whole apparatus so that the vehicle should be carried up an inclined plane. The latter object was readily effected by means of a wedge pushed under the edge of the board opposite to the point where the glass strip was fastened. The wedge was so graduated that in every position it could be seen at a glance what proportion of the distance moved over by the vehicle was movement in a vertical direction. The movement of the vehicle was observed with a microscope of low power, furnished with an eye-piece micrometer. The draw-tube of the instrument was so adjusted that thirty divisions of the eye-piece micrometer corresponded to one m.m. in the field of vision. A stop-watch was used to determine the time occupied by a chosen point on the vehicle in passing over these thirty micrometer divisions.

It will thus be seen that the data of observation in our problem were as follows:—

a = grade per cent. ; *i.e.*, the movement in a vertical direction expressed as a percentage of the distance moved, and determined by a simple observation of the position of the wedge.

b = weight in grammes of the vehicle and the load placed upon it.

c = time occupied by the vehicle in moving one m.m.

d = area in $\frac{60}{c.m.}^2$ of the surface of the vehicle applied to the ciliated membrane.

The value to be determined by means of these observations was the amount of mechanical work, expressed in grammillimetres, which was performed by one square centimetre of ciliated membrane in one minute. If we express this value by x we shall have the formula,—

$$x = \frac{a}{100} \times b \times \frac{60}{c} \times \frac{1}{d} = \frac{6ab}{10cd}.$$

This formula expresses, of course, only the work done in raising the vehicle with its load. A certain amount of work is also performed in overcoming the friction of the vehicle on the membrane; but this amount is very difficult to determine, because the moving force is generated at the same point where the friction is

applied. It is probably small in comparison with the work of raising the vehicle, and it was therefore disregarded.

A modification of the experiment consisted in placing the board in a perpendicular position, so that the vehicle, held in contact with the membrane by capillary attraction, was carried vertically upward. In this case $a = 100$, and the above formula becomes $x = \frac{60b}{c.d}$. In order to obtain as great uniformity as possible in these observations, it was, of course, important to avoid drying of the membrane. For this purpose a 0.5 per cent. solution of common salt, made very slightly alkaline with sodic hydrate, was applied from time to time to the membrane. The results were nevertheless by no means so uniform as could be desired. The following table may serve as an example of the experiments. In this case the grade was at first kept constant at ten per cent., and weights of five, ten, and twenty grammes placed successively upon a vehicle weighing 0.534 gramme. Afterward the board was placed in a vertical position, and observations made on the rate at which the vehicle alone was carried upward.

<i>a.</i> Grade. Per cent.	<i>b.</i> Weight. Grammes.	<i>c.</i> Time. Seconds.	<i>d.</i> Area. $\frac{1}{2}$ c.m.	$x = \frac{60b}{10cd}$ Grammillimetres.
10	10.534	10.8	1.437	4.074
10	10.534	7.4	1.437	5.940
10	20.534	15.	1.437	5.718
10	0.534	3.	1.437	0.743
10	5.534	5.6	1.437	4.127
10	5.534	5.	1.437	4.622
10	10.534	8.5	1.437	5.176
10	20.534	12.6	1.437	6.805
10	20.534	12.6	1.438	6.805
100	0.534	5.3	1.437	4.208
100	0.534	4.2	1.437	5.310
100	0.534	3.8	1.437	5.868
100	0.534	4.4	1.437	5.067
100	0.534	4.8	1.437	4.646
100	0.534	5.	1.437	4.460
100	0.534	5.	1.437	4.460

It will be seen from the table, that by loading the vehicle the rapidity of its movement was diminished, but not in proportion to the increase of the weight. In other words, the greatest amount of work was obtained with the heaviest load. Thus the cilia, when compelled to carry a weight of 20.534 grammes up a grade of one in ten, performed, in one minute for each square centimetre of surface, an amount of work equal to 6.805 grammillimetres. This was the maximum of work obtained in upward of one hundred observations made with various weights and grades; but it is not probable that it is the maximum of work which cilia are capable of performing. It is perfectly possible that under somewhat different con-

ditions they may work to much better advantage. It will be noticed, for instance, in the above table, that when carrying the unloaded vehicle vertically, they performed an amount of work nearly equal to the maximum obtained in carrying heavy weights up an inclined plane. It is not improbable that by altering the size, weight, or shape of the vehicle, conditions may be found under which the cilia may perform a greater amount of work than that here recorded. The investigation of this question will be the subject of a future series of experiments.

The statement that a ciliated membrane performs per square c.m. per minute, 6.805 grammillimetres of work, gives a very imperfect idea of the force of the moving cilia, unless we obtain a conception of the bulk of the organs where this force is generated. It is generally believed, though not absolutely demonstrated, that the force which moves the cilia is generated in the protoplasm of the ciliated cells. These cells in the frog's mouth are spherical in form, with the cilia upon one side. The average of nine measurements gave a diameter of 0.016 m.m., which agrees very well with Valentin's figures. If we imagine spherical cells of this size placed close together on the surface of the membrane, the volume of the cells on one square centimetre of surface will be 1.6 cubic millimetres, and their weight, if we suppose them to have the specific gravity of water, will be 0.0016 gramme. Thus we see that a mass of protoplasm weighing 0.0016 gramme performs in one minute an amount of work equal to lifting 6.805 grammes to the height of one millimetre. This is equal to lifting 0.0016 gramme to the height of 4253 millimetres. In other words, the ciliated cells perform in one minute an amount of work equal to lifting their own weight to the height of 4.253 metres. It is interesting to compare this value with that obtained for the striated muscles of the heart. The work performed by the heart at each pulsation is equal to the weight of the blood expelled by the contraction multiplied by the height of a column of blood which measures the tension in the aorta and pulmonary arteries. From these data Schiff (*Physiologie de la Digestion*, i. 24) has estimated that the heart does in one minute an amount of work equal to lifting its own weight to the height of one hundred and fifty metres, a value more than thirty-five times as great as that above given for the ciliated epithelium.—*Boston Medical and Surgical Journal*, 10th August.

Part Fourth.

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